Winter Diet and Hunting Success of Canada Lynx in Colorado

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ABSTRACT Information regarding the diet of Canada lynx (*Lynx canadensis*) at the southernmost extent of its range is critical for managing the species under current and predicted climate conditions. Therefore, from 1999–2009, we investigated winter diet and hunting strategies of Canada lynx in Colorado, USA by tracking individuals in the snow to identify sites where lynx encountered and killed prey. Similar to other parts of lynx range, snowshoe hares (*Lepus americanus*) were the primary winter food in Colorado, especially when considering total biomass consumed. Red squirrels (*Tamiasciurus hudsonicus*) comprised the bulk of the remaining food items and were a substantial occurrence during several years, which is consistent with previous hypotheses regarding the diet of lynx in southerly populations. Lynx successfully captured snowshoe hares on 31% of attempts and red squirrels on 47% of attempts, similar to lynx in other regions. In contrast to other populations, the majority of chases of both prey species were initiated while actively hunting rather than by ambush and this behavior did not change through time. We found evidence for snowshoe hare refugia during winter; hunting success for hares peaked at sites with approximately 3,000 stems/ha, but was lower in more dense vegetation where hare densities were greater. Given this finding and the apparent importance of red squirrels as alternate prey, we suggest that management for lynx in the southern Rocky Mountains, USA, focus on maintenance of mature, uneven-aged Engelmann spruce (*Picea engelmannii*)-subalpine fir (*Abies lasiocarpa*) stands. Such stands naturally provide patches of dense and open habitats juxtaposed closely together that should simultaneously facilitate high hare densities (and refuge from predation) and accessibility to hares by lynx. Mature trees in such stands also provide abundant cone crops to sustain populations of red squirrels for use as alternate prey. © 2016 The Authors. *Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

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The Canada lynx (*Lynx canadensis*) is a dietary specialist whose occurrence and life history are intimately linked to its primary prey, the snowshoe hare (*Lepus americanus*; Koehler and Aubry 1994, Aubry et al. 2000, Mowat et al. 2000). The relationship between the 2 species is thought to be strongest in northern populations (i.e., those populations that occur in boreal forests of Canada and Alaska) where lynx and hare populations are strongly cyclic. In boreal forests, winter diet of lynx is comprised almost exclusively of snowshoe hares (e.g., frequency of occurrence in scats or kill sites is 85–100%) when hares are abundant (Saunders 1963, Brand et al. 1976, O'Donoghue et al. 1998*b*); lynx switch to alternate prey, such as red squirrels (*Tamiasciurus hudsonicus*), when hares become rare (e.g., frequency of occurrence of hares in scats or kills drops to ~10–83%; Brand et al.

1976, O'Donoghue et al. 1998*a*, *b*). Concurrently, when hares become rare, lynx tend to switch their hunting behavior from stalking prey to hunting from ambush beds (O'Donoghue et al. 1998*a*), which may (Murray et al. 1995) or may not (O'Donoghue et al. 1998*a*) improve their hunting success, but probably serves to conserve energy during periods of scarce resources (O'Donoghue et al. 1998*a*). Despite the switch in diet and hunting strategy, snowshoe hares comprise the bulk of winter diet items in most years, and by biomass they almost always comprise a majority of the diet even during years when alternate prey are consumed more often (Brand et al. 1976, O'Donoghue et al. 1998*b*). Furthermore, lynx survival and productivity decline sharply following declines in snowshoe hares, illustrating the pivotal role hares play in the dynamics of northern lynx populations despite the ability of lynx to use alternate prey (Poole 1994, Mowat et al. 1996, Slough and Mowat 1996, O'Donoghue et al. 2001).

Because snowshoe hare densities at the southern periphery of lynx–hare range (i.e., southern Canada and the contiguous United States) most resemble northern populations during cyclic lows, Apps (2000) hypothesized that southern lynx

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populations should be characterized by a diet that includes substantial alternate prey (i.e., red squirrels). Results from snow tracking in southeast British Columbia and southwest Alberta, Canada were consistent with this hypothesis; 47% of kills were items other than snowshoe hares (Apps 2000). Similarly, alternate prey comprised a significant portion of scat contents during winter in Washington (24–28% red squirrel; Koehler 1990, Von Kienast 2003). Based on a range-wide analysis of stable isotopes, Roth et al. (2007) concluded that lynx specialize more on snowshoe hares with increasing latitude and use more alternate prey, such as red squirrels, at southern localities. However, over 4 winters in Montana, snowshoe hares comprised 96% of the biomass in lynx diet; red squirrels and other alternate prey were unimportant and taken only opportunistically (Squires and Ruggiero 2007). Furthermore, in Nova Scotia, snowshoe hares dominated lynx diet by occurrence during winter (93% of items in scat samples were snowshoe hares; Parker et al. 1983), and in Maine, recent evidence suggests that characteristics of the lynx–hare system align closely with northern populations (Vashon et al. 2008a, b). Thus, evidence that the winter diet of lynx is broader in southern portions of its range, where they are listed as threatened by the United States Fish and Wildlife Service (2000), has been somewhat inconsistent.

In northern populations, snowshoe hares persist in patches of high-quality habitat as predation increases during declining and low phases of the lynx–hare cycle (Keith 1966, Wolff 1980). These patches are typified by dense vegetation that provides abundant food and cover. Additionally, these patches offer refuge from heavy predation by lynx and serve as sources for population recovery after lynx numbers subside (Wolff 1980). Thus, refugia for hares are a critical component of lynx–hare ecology. In fact, although empirical evidence suggests that the lynx–hare cycle is influenced largely by predation and food limitation (Krebs et al. 1995, 2001), recent theoretical work suggests that the existence of hare refugia alone can lead to models of predator–prey dynamics that account for all of the characteristics of the dynamic lynx–hare relationship (Chivers et al. 2014). Refugia clearly exist in the southern population of Maine also; hares select for stands with high stem density, but lynx choose to forage in stands where stem density is intermediate and hares are more accessible (Fuller et al. 2007). However, in Montana and Washington (also southern populations), lynx hunted in stands where hare densities were highest (Squires and Ruggiero 2007, Maletzke et al. 2008), indicating a lack of refugia, at least with respect to lynx predation. Perhaps, strong differences in stem densities between the regions (3,496 stems/ha in Washington vs. >14,000 stems/ha in some stands in Maine) accounts for the disparate evidence for refuge habitat among southern populations.

Given that lynx and snowshoe hares are adapted to cold, snowy, and high-elevation or high-latitude environments, they are both species of concern with respect to climate change. Current modeling suggests that the range of boreal forests and persistent snow will diminish, especially at the southern distributional limits for lynx and snowshoe hares (Pierce and Cayan 2013, Fisichelli et al. 2014). However, current models also predict that extensive areas of lynx habitat in the southern Rocky Mountains, USA may persist because impacts to these high-elevation subalpine forests are expected to be moderate compared to impacts to lower elevation systems (McKelvey et al. 2011, Decker and Fink 2014, Peers et al. 2014). Furthermore, the predicted effects of climate change might be mitigated if lynx in this region can successfully expand their diet, given that the range of red squirrels is expected to remain somewhat robust to climate change compared to that of snowshoe hares (Peers et al. 2014). Thus, an examination of lynx diet at their southern range limit and a determination of their ability to use alternate prey are important factors in conservation planning for the species.

Lynx occurred historically in Colorado (McKelvey et al. 2000) but were apparently extirpated by the early 1970s (Meaney 2002). The Colorado Division of Wildlife (now Colorado Parks and Wildlife) translocated lynx from Canada and Alaska into Colorado from 1999–2006 (Devineau et al. 2010). At the conclusion of the reintroduction effort in 2010, Shenk (2010) estimated that the population would sustain itself given survival and productivity patterns observed during the previous decade. Furthermore, occupancy was largely unchanged from the end of the reintroduction through winter 2014–2015 (Ivan et al. 2015). Thus, we presently consider the lynx population in Colorado to be established and secure. Colorado represents an extreme peninsular extension of the southern range limit for lynx and snowshoe hares, but contains over 1.8 million ha of habitat (Ivan et al. 2011) that may resist climate change better than expected because of its high elevation. Thus, Colorado could prove to be important for recovery and resiliency of lynx, yet no information exists regarding their local diet, hunting patterns, or management actions that could optimize their hunting efficiency.

Our goal was to describe winter diet and hunting habits of lynx in Colorado for comparison with work conducted throughout the species range and to provide local managers with reliable information upon which to make decisions. We focused on winter diet because most of the comparative literature characterizes winter diet only and winter diet likely contributes most directly to body condition during the breeding season, which occurs in mid–late winter. In addition to describing diet and hunting habits, we also tested for the existence of refugia. Generally, we wanted to differentiate among the following broad hypotheses: diet and hunting characteristics of lynx in Colorado should 1) reflect those of northern populations during cyclic lows (i.e., diet contains significant portions of prey other than snowshoe hares, refugia exist), especially because reintroduced individuals were obtained from northern populations; 2) reflect lynx populations in Montana, the closest Rocky Mountain population, where evidence for refugia is lacking and lynx do not make significant use of alternate prey; or 3) reflect a blending of these characteristics that may have changed through time as lynx from northern populations have

acclimated and adapted to conditions in the southern Rocky Mountains.

STUDY AREA

We assessed diet and hunting success of Canada lynx in southwest and central Colorado, USA, primarily in the San Juan and Sawatch mountain ranges. However, we also tracked individuals that colonized the Central Front Range, Elk Mountains, and Grand Mesa (Fig. 1). Lynx occurred primarily on public lands managed by the United States Forest Service and Bureau of Land Management.

Sagebrush (*Artemisia* spp.) parks dominated relatively low-elevation (1,200–2,500 m) valleys that heavily dissected the study area. Montane forest vegetation (1,700–2,700 m) consisted largely of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*). Subalpine forests (2,700–3,500 m) in the San Juan Mountains and Grand Mesa were comprised of Engelmann spruce (*Picea engel-mannii*) and subalpine fir (*Abies lasiocarpa*) with aspen (*Populus tremuloides*), high meadows, and willow (*Salix* spp.) carrs intermixed. In addition, subalpine forests elsewhere in the study area included significant stands of climax (drier sites) or seral (moister sites) lodgepole pine (*Pinus contorta*). Alpine tundra and rocky peaks topped the highest elevations (3,500–4,200 m). The majority of lynx use (and thus our sampling efforts) occurred within forests composed of a mixture of Engelmann spruce and subalpine fir.

Mean July temperature on the study area was 13° C; mean January temperature was −10° C (National Oceanic and Atmospheric Administration 2015). In the subalpine zone where sampling occurred, snow cover generally persisted from November through May or June and maximum snow depth during the study averaged 146 cm (Natural Resources Conservation Service 2015). Other predators in the study area that may have directly or indirectly affected diet choices of lynx included coyotes (*Canis latrans*), cougars (*Puma concolor*), bobcats (*Lynx rufus*), red foxes (*Vulpes vulpes*), black bears (*Ursus americanus*), American martens (*Martes americana*), northern goshawks (*Accipter gentilis*), and great-horned owls (*Bubo virginanus*).

METHODS

Sampling

From 1999–2006, the Colorado Division of Wildlife (CDOW) released 218 wild-caught lynx from Canada and Alaska into Colorado. Forty-six lynx released in 1999 and 2000 were instrumented with very high frequency (VHF) transmitters (Telonics™, Mesa, AZ, USA). All remaining lynx released in 2000 and those released from 2001 to 2006 were instrumented with dual platform transmitter terminal (PTT) and VHF collars (Sirtrack™, Havelock North, New Zealand). We made an annual effort to trap and re-collar (using dual PTT and VHF collars) individuals to maintain as many working telemetry transmitters as possible. All capture and handling procedures were approved by CDOW Animal Care and Use Committee (ACUC Protocol #04-2000). The PTTs were active for a single 12-hour block each week during which 1–21 locations were recorded ($\bar{x} = 2.7$ locations/12-hr block). Aerial flights to locate individuals via VHF typically occurred once per week during winter.

Crews tracked lynx in the snow from February through mid-May 1999, and approximately December through March or April each winter from 1999–2000 through 2008–2009. We used weekly telemetry locations to determine where to search for tracks on the ground. Most tracking areas were accessed via snowmobile 1–4 days following a location. We used Argos locations of class 1–3, aerial VHF, and ground-based VHF on the day of tracking to assign known individuals to tracks. Lynx living primarily in wilderness or roadless areas were rarely sampled due to inaccessibility. We assumed that diet and hunting characteristics did not differ appreciably between lynx living in wilderness areas and those residing outside of wilderness because management activity (e.g., timber harvest) in the areas we sampled was relatively light. Each winter, we attempted to sample as many individuals as possible and to spread this effort evenly across individuals and throughout the study area. However, because of differences in accessibility, survival, collar life, long-distance movements, and logistics, we were unable to sample individuals equally. For example, 10 lynx (7%) were sampled on >30 occasions and 12 (9%) only once. The majority (70 individuals, 53%), however, were sampled on 5–25 occasions and overall, individuals were sampled an average of 11.7 times. Thus, our effort was representative of lynx hunting habits in the area and was not overly influenced by outlier individuals tracked very frequently or very infrequently.

Once crews discovered tracks, they generally back-tracked but forward-tracked if telemetry signals indicated the lynx was no longer in the area or distant enough that their behavior would unlikely be influenced by trackers. When crews encountered a site marking the start of a chase (i.e., where tracks indicated that the lynx had discovered prey and
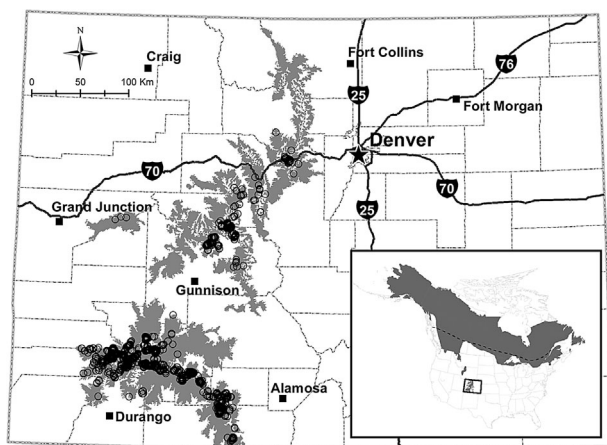
Figure 1. Gray shaded area is the approximate area where we examined the diet of Canada lynx in Colorado, USA. Open circles indicate where we tracked lynx during February through mid-May 1999, and December 1999 through April 2009. Inset: Range of Canada lynx and approximate boundary (dashed line) between northern and southern populations.

both animals abruptly erupted into bounding gaits), they recorded Universal Transverse Mercator (UTM) coordinates, aspect, slope, and elevation. Chases were assumed to be successful (i.e., ultimately ended in a kill) if tracks indicated that the prey was overtaken by the lynx or if remains of dead prey were discovered at the end of the chase. Prey species were identified by tracks and/or remains at the kill site. At a subset of sites where evidence was unambiguous, crews recorded whether the chase was initiated from a bed (i.e., bounding after prey started immediately from a crouched, stationary position) or while the lynx was actively hunting. In addition to sites of interest for this work (i.e., initiation of chases), crews also recorded coordinates for the beginning and end of their tracking session and other sites of interest (i.e., territory marks, road crossings, beds). We used locations of all such sites to estimate the distance tracked each day.

From 2000–2006, crews sampled vegetation where chases were initiated using a 5×5 grid of sample points (3-m spacing) centered at the site. At each of the 25 points, crews recorded snow depth, understory cover (0 or 1 indicating whether a tree, shrub, or coarse wood intersected a column 6-cm in diameter rising above the snow to 150 cm), understory density (no. tree, shrub, or coarse wood branches intersecting the 6-cm column at half-meter intervals above the snow to 150 cm), and overstory cover (0 or 1 indicating whether a tree, shrub, or coarse wood intersected the crosshair of a densitometer at each point). Crews also tallied the number of trees (stem density) that protruded through the snow surface within the 144-m^2 plot.

Crews initially tallied understory, understory cover, and overstory measurements by species, but given that 90% of all chase sites occurred within spruce-fir forests, we merged all species together for analysis. The only exception was that we noted the presence of a willow component when it occurred at the site because previous anecdotal evidence from the area (Shenk 2005) and elsewhere (Mowat and Slough 2003) suggests that hares, and thus lynx, may select for willow components where available. Also, we excluded 7 sites that occurred in pure willow thickets so dense that they precluded tracking and measurement. We recognize that exclusion of the densest sites from our analysis may have introduced bias into the results. However, these sites were relatively few (0.9% of total sites where chases were initiated) and differed markedly in structure and composition from the majority of other sites. We assume that our results are informative and pertinent to the majority of lynx habitat in the study area.

Analysis

To describe the winter diet and hunting patterns of lynx in Colorado for comparison with other regions, we tallied the frequency of occurrence of snowshoe hares and red squirrels recorded at kill sites by year based on the pooled number of kills across individuals. We also converted occurrence data to percent biomass by assuming that the average mass consumed from each snowshoe hare and red squirrel was 1,250 g and 225 g, respectively (Armstrong et al. 2011). Occasional other prey included mountain cottontail (*Sylvilagus nuttallii*; $n = 10$), white-tailed

ptarmigan (*Lagopus leucura*; $n = 2$), gray jay (*Perisoreus canadensis*; $n = 2$), American marten (*Martes americana*; $n = 2$), mice (*Peromyscus* spp.; $n = 2$), white-tailed jackrabbit (*Lepus townsendii*; $n = 1$), mule deer (*Odocoileus hemionus*; $n = 1$ hindquarter of a yearling), ermine (*Mustela erminea*; $n = 1$), dusky grouse (*Dendragapus obscures*; $n = 1$), and woodpeckers (*Picoides* spp.; $n = 1$). We included published weights of these species in calculations of lynx diet by biomass (Armstrong et al. 2011, Cornell Lab of Ornithology 2016). We also calculated kill rate (kills identified/km tracked), overall hunting success (no. kills/ no. chases), and hunting success from a bed compared to stalking for both snowshoe hares and red squirrels.

To assess the existence and structure of refugia in the study area, we used package lme4 (Bates et al. 2015) in R (R Development Core Team 2015) to fit logistic regression models relating hunting success to a suite of covariates measured where the chase initiated. This analysis was limited to 2000–2006 because these were the only years that we collected vegetation data at chase sites. We initially considered all vegetation measurements taken at each site as potential predictors of success. However, understory cover and understory density were highly correlated ($r = 0.72$), and measure much the same phenomenon as stem density (although we note that mature trees may count little toward stem density but more toward understory if they have thick lower branches near the snow surface). To simplify the number of parameters (and models) under consideration and avoid redundancy in model construction, we chose to retain stem density as a broad representation of cover, and discarded understory cover and understory density from further analysis. Of these measurements, stem density is most compatible with metrics routinely collected and used by forest managers and by previous researchers. We also considered (stem density)^2 as a potential predictor variable to allow for the possibility that hunting success may be highest at intermediate stem densities, as reported elsewhere (e.g., Fuller et al. 2007). We retained overstory as a potential predictor because it has a direct impact on understory, can affect overall visibility at a site, and is a proxy for escape cover for red squirrels. We included (overstory)^2 to allow for the existence of non-linear relationships. Because we sampled individuals repeatedly but unequally and expected average hunting success to vary by individual attributes (e.g., age, sex, origin of translocation), we included individual lynx as a random intercept in each model. We included individual year effects as potential predictor variables to allow for variation in environmental conditions on an annual basis. We also included year as a linear trend to allow for the possibility that hunting success generally increased or decreased linearly as the reintroduction progressed.

We initially considered a model set containing all possible combinations of the 7 variables described above (year, trend across years, stem density, [stem density]^2, overstory, [overstory]^2, and willow). However, we omitted models in which squared terms occurred without inclusion of lower order terms, and we only allowed 1 type of year effect in any given model. This resulted in a final set of 54 candidate

Table 1. Percent occurrence (% biomass) of snowshoe hares, red squirrels, and other prey items in the winter diet of Canada lynx in Colorado, USA, 1999–2009.

Winter	No. lynx tracked	Total km tracked	Total kills	Snowshoe hare (%)	Red squirrel (%)	Other (%)
1999	12	157	6	67 (92)	33 (8)	0 (0)
1999–2000	19	493	68	72 (84)	22 (5)	6 (12)
2000–2001	47	611	77	65 (84)	22 (5)	13 (11)
2001–2002	32	388	42	90 (97)	7 (1)	2 (2)
2002–2003	27	557	50	88 (97)	8 (2)	4 (2)
2003–2004	33	403	36	69 (91)	28 (7)	3 (3)
2004–2005	42	520	65	86 (97)	12 (2)	2 (1)
2005–2006	45	485	67	88 (98)	9 (2)	3 (1)
2006–2007	32	357	36	56 (87)	44 (13)	0 (0)
2007–2008	25	345	46	59 (89)	39 (11)	2 (0)
2008–2009	25	296	53	26 (65)	72 (32)	2 (4)
$\bar{x}$	31	419	50	70 (89)	27 (8)	3 (3)

models. We considered the same model set for both snowshoe hare and red squirrel chases. However, willow rarely occurred at sites where red squirrel chases were initiated and including this effect caused model-fitting algorithms to fail. Thus, for the red squirrel analysis, we removed any model that included willow (27 candidate models remained). For both snowshoe hare and red squirrel data sets, we conducted model selection using Akaike's Information Criterion (AIC; Burnham and Anderson 2002) and made inference based largely on those models within 2 AIC units of the top model.

RESULTS

We tracked 132 lynx for 4,612 km across 11 winters. We documented 1,746 chases and 546 kills (Table 1). Overall, snowshoe hares comprised the majority of winter diet by occurrence ($\bar{x} = 70\%$, range = 26–90%), but in 7 of 11 years, red squirrels comprised at least 20% of the diet, and during the final year of the study, lynx diet consisted of 72% red squirrels (Table 1). By biomass, snowshoe hares were the most significant prey species for lynx across all years ($\bar{x} = 89\%$, range = 65–98), even during winters when lynx killed a higher proportion of red squirrels. Other species comprised relatively insignificant portions of the diet (3% occurrence, 3% biomass; Table 1).

Once a chase was initiated, lynx were more successful at capturing red squirrels than hares (Table 2). Regardless of prey species, lynx hunted via stalking more often than they attempted to capture prey from a bed, and they were generally more successful while stalking than from a bed (Table 2). From year to year, hunting success was variable for both snowshoe hares (range = 18–54%) and red squirrels (range = 33–75%), but the primary hunting method remained fairly consistent across years (lynx stalked hares on 89–98% of hunting occasions; lynx stalked red squirrels on 76–100% of occasions; Table 2). We estimated that lynx killed on average 0.08 (95% CI = 0.06–0.09) hares for every km traveled (1 hare/12.5 km) and 0.03 (95% CI = 0.01–0.05) red squirrels for every km traveled (1 red squirrel/33.3 km; Table 2).

For snowshoe hares, the top model relating hunting success to habitat included additive effects for year, stem density, (stem density)^2, and presence of willow (Table 3). Hunting success was highest for the second winter analyzed (2001–2002) and lowest for the last winter (2005–2006), although confidence intervals slightly overlapped 0 for all years. The presence of willow at the site where a chase began was associated with an increase in hunting success ($\beta = 0.67$, 95% CI = −0.05 to 1.39). Hunting success peaked at approximately 3,000 stems/ha and declined dramatically

Table 2. Hunting success (% of chases initiated) of Canada lynx for 2 primary prey items in Colorado USA, 1999–2009.

	Snowshoe hare					Red squirrel				
			% success					% success		
Winter	Chases	Kills/km	Overall	Stalking	From bed	Chases	Kills/km	Overall	Stalking	From bed
1999	21	0.03	19	21 (90)	0 (10)	6	0.01	33	33 (83)	100 (17)
1999–2000	113	0.10	43	46 (90)	27 (10)	29	0.03	52	68 (76)	29 (24)
2000–2001	129	0.08	39	38 (98)	50 (2)	22	0.03	77	84 (91)	0 (9)
2001–2002	72	0.10	53	54 (96)	0 (4)	4	0.01	75	75 (100)	0 (0)
2002–2003	145	0.08	30	31 (90)	21 (10)	12	0.01	33	36 (92)	0 (8)
2003–2004	86	0.06	29	30 (89)	11 (11)	21	0.02	48	59 (81)	0 (19)
2004–2005	208	0.11	27	27 (92)	31 (8)	14	0.02	57	55 (79)	67 (21)
2005–2006	189	0.12	31	32 (92)	20 (8)	15	0.01	40	46 (93)	0 (7)
2006–2007	102	0.06	20	18 (90)	20 (10)	32	0.04	50	48 (69)	50 (31)
2007–2008	113	0.08	24	25 (97)	0 (3)	49	0.05	37	39 (94)	33 (6)
2008–2009	80	0.05	18	18 (95)	0 (5)	86	0.13	44	43 (91)	63 (9)
$\bar{x}$	114	0.08	30	31 (93)	16 (7)	26	0.03	50	53 (86)	31 (14)

Table 3. Model selection results for hunting success of Canada lynx on snowshoe hares as a function of vegetation attributes at the site where the chase began, Colorado, USA, 2000–2006. We compared 54 models and present the top 10 based on Akaike's Information Criterion (AIC). We also present the difference between the AIC score of each model relative to the best (minimum score) model (ΔAIC), the probability that a model is the best in the set given the data and model set under consideration (w_i), and the number of parameters in the model (K), including the random intercept for individuals. T indicates that a year effect was included as a linear trend through time, whereas t indicates that each year was allowed to have its own additive effect.

Model	AIC	ΔAIC	w_i	K
Year(t) + stem density + stem density^2 + willow	877.0	0.0	0.16	10
Year(t) + stem density + stem density^2	878.3	1.3	0.09	9
Year(t) + stem density + stem density^2 + overstory + willow	878.3	1.3	0.08	11
Year(t) + willow	879.1	2.1	0.06	8
Year(t) + stem density + stem density^2 + overstory	879.2	2.2	0.05	10
Year(t) + stem density + willow	879.3	2.2	0.05	9
Year(t) + stem density	879.7	2.7	0.04	8
Year(t)	879.7	2.7	0.04	7
Year(T) + stem density + stem density^2 + willow	879.9	2.9	0.04	6
Year(t) + stem density + stem density^2 + overstory + overstory^2 + willow	880.1	3.1	0.03	12

beyond 6,000 stems/ha (Fig. 2; $\beta_{stem\ density} = 2.41$, 95% CI $= -0.79$ to 5.62; $\beta_{stem\ density}^2 = -4.25$, 95% CI $= -8.62$ to 0.12). Other models within 2 AIC units of the top model, and most of those within the top 10 models (≤ 3.1 ΔAIC), had structures that were nested within the top model (Table 3). Two models in the top 10 included an effect for overstory cover, but the addition of overstory actually worsened the AIC score compared to the base model without it, and the 95% confidence intervals for the coefficient for overstory substantially overlapped 0 (e.g., when included with stem density: $\beta = -0.40$, 95% CI $= -1.35$ to 0.55). Thus, it added little information and was a poor predictor of hunting success.

The top model relating red squirrel hunting success to habitat included additive effects of year (linear trend) and overstory cover (Table 4). Hunting success declined linearly through time ($\beta = -0.36$, 95% CI $= -0.64$ to -0.08) and was positively associated with overstory cover ($\beta = 2.00$, 95% CI $= -0.51$ to 4.51). Other models within 2 AIC units of the top model included additional variables, but similar to

above, addition of these variables increased AIC scores compared to base models without them indicating they added little information.

DISCUSSION

In general, snowshoe hares comprised the bulk of Canada lynx winter diet in Colorado by occurrence, and dominated the diet by biomass in all years. Hare occurrence peaked in the diet from 2001 to 2006, whereas red squirrels peaked in occurrence opposite of hares during the first and last 3 years of the study (but note 2003–2004 as an exception to this pattern). During several winters, the red squirrel portion of the diet topped 20% by occurrence and even comprised a third of the diet by biomass during the last winter. In one portion of the study area, Ivan et al. (2014) documented a decline in snowshoe hare density in spruce-fir stands during winters of 2006–2007 and 2007–2008 followed by a partial recovery during 2008–2009. Thus, the apparent shift in occurrence from hares to squirrels during the final years of the study may have been precipitated by a reduction in their primary prey source. Conversely, anecdotal evidence suggested that red squirrel numbers peaked during these last years, so lynx may have simply taken advantage of an abundant resource. Although hunting success for snowshoe hares was lower during these later years, the proportion of chases initiated from beds remained low and did not change throughout the study. Thus, lynx did not appear to alter their hunting strategy in response to apparent changes in prey abundance as has been shown in northern populations (Murray et al. 1995, O'Donoghue et al. 1998a). Rather, they simply adjusted their diet to include more alternate prey items.

The winter diet of lynx in Colorado were heavily skewed toward snowshoe hares as has been documented throughout lynx range (Van Zyll de Jong 1966, Brand et al. 1976, More 1976, Parker et al. 1983, Squires and Ruggiero 2007). However, the substantial proportion of red squirrel in winter diet we observed also aligns with hypotheses regarding increased dietary breadth of southern lynx populations (Apps 2000), and empirical results from diet studies in this part of the range (Koehler 1990, Apps 2000, Roth et al. 2007). Notably, our results stand in contrast to results from
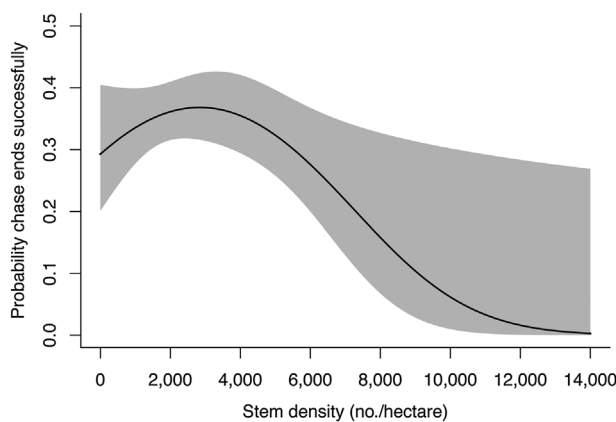
Figure 2. Probability that a Canada lynx captured a snowshoe hare as a function of the stem density (trees/ha) at the site where the chase began. The relationship is based on the top model in the set we considered based on Akaike's Information Criterion; all other covariates in the model were fixed to their mean level. The gray shaded area is the 95% confidence interval. We sampled lynx throughout southwest and central Colorado during February through mid-May 1999, and December 1999 through April 2009.

Table 4. Model selection results for hunting success of Canada lynx on red squirrels as a function of vegetation attributes at the site where the chase began, Colorado, USA, 2000–2006. We compared 27 models and present the top 10 based on Akaike's Information criterion (AIC). We also present the difference between the AIC score of each model relative to the best (minimum score) model (ΔAIC), the probability that a model is the best in the set given the data and model set under consideration (w_i), and the total number of parameters in the model (K), including the random intercept for individuals. T indicates that a year effect was included as a linear trend through time, whereas t indicates that each year was allowed to have its own additive effect.

Model	AIC	ΔAIC	w_i	K
Year(T) + overstory	104.5	0.0	0.15	4
Year(T)	105.0	0.5	0.12	3
Year(T) + stem density + stem density^2 + overstory	105.0	0.5	0.11	6
Year(T) + overstory + overstory^2	106.3	1.8	0.06	5
Year(t) + stem density + stem density^2 + overstory	106.4	1.9	0.06	10
Year(T) + stem density	106.5	2.0	0.06	4
Year(T) + stem density + overstory	106.5	2.0	0.06	5
Year(t)	106.7	2.2	0.05	7
Year(T) + stem density + stem density^2	106.8	2.3	0.05	5
Year(T) + stem density + stem density^2 + overstory + overstory^2	107.0	2.5	0.04	7

Montana, the closest study area geographically to ours, where red squirrels were taken by lynx more infrequently and nearly half of predation attempts occurred from beds (Squires and Ruggiero 2007). Our occurrence data suggested a shift from relatively high (>20%) use of red squirrels, to relatively low use ($\leq$12%), then back to high use, which reflects results obtained from highly cyclic lynx–hare systems in Yukon Territory (O'Donoghue et al. 1998*b*), although less dramatic. Like O'Donoghue et al. (1998*b*), we also documented consistent preference for snowshoe hares by biomass, even through bouts of apparent prey switching as indexed by percent occurrence.

Overall hunting success (31%) for snowshoe hares was within the range of that reported elsewhere (Nellis and Keith 1968, Koehler 1990, Murray et al. 1995, O'Donoghue et al. 1998*b*). However, high overall success rates (47%) for red squirrels were matched only by lynx in Yukon Territory, Canada (O'Donoghue et al. 1998*b*). The kill rate of snowshoe hares in Colorado (0.08 kills/km) was lower than that reported for lynx in central Alberta, Canada (0.15–0.55 kills/km; Brand et al. 1976), Nova Scotia, Canada (0.13 kills/km; Parker et al. 1983), and Montana, USA (0.12 kills/km; Squires and Ruggiero 2007). Lower kill rates in Colorado could be due to overall lower densities of snowshoe hares in the region (mean winter hare densities in spruce-fir forests from 2006–2009 were 0.05–0.21 hares/ha; Ivan et al. 2014), which would require more travel to obtain the same number of prey. Alternatively, perhaps the increased patchiness of the southern Rocky Mountain landscape (Dolbeer and Clark 1975, Wolff 1980) necessitated more travel (across vegetation types that do not provide habitat for snowshoe hares) to access a similar number of hunting patches compared to more continuous habitat farther north.

We found that the winter diet and hunting characteristics of lynx in Colorado were a blend of characteristics common to all lynx populations (e.g., snowshoe hares comprise the majority of the diet in most years, especially by biomass), characteristics more closely aligned to northern populations (e.g., over the course of the 11-year study, lynx shifted the proportion of their diet allocated to red squirrels and snowshoe), and elements that have been hypothesized to be unique to southern populations (e.g., in most years, red squirrels comprised a substantial portion of the diet). It is plausible that lynx in our study area exhibited this blending of diet and hunting characteristics because they were translocated from northern populations (Quebec, Manitoba, British Columbia, Yukon Territory, and Alaska) into the extreme southern limit of lynx range. However, our study occurred over a decade and included 14 Colorado-born individuals, 3 winters of data collection after the release of the last individual, and numerous cases in which individuals were tracked >5 years after they were translocated. Thus, we feel that the individuals in this study had ample time to acclimate to local conditions in Colorado and their hunting preferences likely reflect behavioral responses to those local resources rather than hunting strategies formed prior to being translocated. O'Donoghue et al. (1998*b*) documented a lag of up to a year in prey-switching by lynx; individuals that had grown used to preying on red squirrels continued to do so for an extra winter, even when hare numbers began to increase. That this strong focus on red squirrels lasted only 1 year supports our claim that our results reflect resident animals responding to current, local conditions rather than individuals exhibiting habits formed previously.

Peers et al. (2014) suggested that the ability of lynx to cope with a changing climate will be in part related to their capacity to successfully include red squirrels in their diet. This is because the impacts of climate change on the retraction of red squirrel habitat at the trailing edge of lynx range is expected to be less dramatic than that of snowshoe hares (Peers et al. 2014). Our findings indicate that lynx are capable of exploiting red squirrels in Colorado when they are readily available or when snowshoe hares are relatively sparse. We also documented successful reproduction in 2009 after a winter of heavy reliance on red squirrels (Shenk 2009). However, prevailing evidence suggests that lynx reproduction and recruitment will suffer in the long term when their diet is consistently skewed toward red squirrels and deficient in snowshoe hares (Poole 1994, Mowat et al. 1996, Slough and Mowat 1996, O'Donoghue et al. 2001). Furthermore, a number of factors other than prey-switching will likely affect the ability of lynx to cope with climate change. For instance, extensive bark beetle outbreaks are currently affecting

spruce-fir systems in Colorado and beyond. This is likely to have a large-scale, negative impact on red squirrels due to a reduction in cone-producing trees (Ivan and Seglund 2015). Also, prolonged mismatch between the environment and pelt color of snowshoe hares due to diminished duration of snow cover could have a drastic population-level impact on that species, which may or may not be alleviated by evolutionary adaption (Zimova et al. 2016). Thus, the ability of lynx to cope with changing future conditions remains questionable.

Our logistic regression analysis for snowshoe hares indicated a quadratic relationship between hunting success and stem density such that capture success peaked at 2,000–4,000 stems/ha and dropped dramatically beyond 6,000 stems/ha. The highest snowshoe hare densities documented by Ivan et al. (2014) in Colorado occurred during summer in late-seral Engelmann spruce-subalpine fir and early seral lodgepole pine stands, which had total stem densities of 5,874 stems/ha and 6,231 stems/ha, respectively (Ivan et al. 2014:Appendix A). During winter, the replicates with the highest snowshoe hare densities averaged 5,828 stems/ha (J. S. Ivan, Colorado Parks and Wildlife, unpublished data). These results suggest that snowshoe hare refugia exist in Colorado; peak hunting success occurred at stem densities below which peak hare density occurred. This pattern stands in contrast to results from Montana, which suggested that lynx select habitat with the highest densities of hares (Squires and Ruggiero 2007). Our results are, however, consistent with lynx hunting behavior documented in Maine (Fuller et al. 2007) and Alaska (Wolff 1980).

We found that the presence of willow at a chase site was positively associated with capture success of snowshoe hares. Ivan et al. (2014) noted that snowshoe hare density on their study site in central Colorado was positively associated with the amount of willow present in the surrounding landscape and negatively associated with distance to the nearest willow patch, although both associations were relatively weak. Shenk (2005) reported that riparian willow zones and edges were a heavily used habitat by lynx, at least during summer. Thus, that willow was associated with snowshoe hare activity is unsurprising. Why willow would facilitate successful capture of hares once a chase begins is unclear, however.

Hunting success for red squirrels was positively correlated with overstory cover. As with snowshoe hares and willow, we expected increased overstory cover (and presumably, increased no. mature trees) to be positively associated with increased abundance of red squirrels because of their reliance on cone crops (Armstrong et al. 2011). However, more mature trees seem likely to provide more escape cover for squirrels, which should hinder capture success. Thus, we see no clear biological mechanism for this relationship.

In summary, our results demonstrate that snowshoe hares are a highly preferred prey item for Canada lynx inhabiting the southern Rocky Mountains, just as they are in more northerly lynx populations. However, we also demonstrated that the diet of lynx in Colorado is flexible enough to accommodate some fluctuation in snowshoe hare and red squirrel abundance. Other diet and hunting patterns of lynx in Colorado were a mix of elements thought to be characteristic of southern populations and those indicative of northerly populations.

MANAGEMENT IMPLICATIONS

Management of winter hunting habitat for Canada lynx in Colorado should include a matrix of vegetation types in which dense patches (>6,000 stems/ha) capable of supporting abundant snowshoe hares are closely juxtaposed with less-dense patches (2,000–4,000 stems/ha) where lynx can more successfully capture prey. Small (<5 ha), regenerating clear cuts scattered within an untreated matrix could produce this type of environment, albeit for a finite period of time when the regenerating stand is of the appropriate height and density. However, we suggest that optimal conditions can be met most effectively by managing for mature, uneven-aged spruce-fir stands, which tend to naturally include small patches of both types juxtaposed at finer scales. Additionally, the large trees within these mature stands, especially subalpine fir, often exhibit a growth form where dense lower branches fan out for some distance along the ground, creating a microhabitat with high horizontal cover in areas where stem density may otherwise be relatively sparse. Thus, thick and moderate cover can be intermingled at an even finer sub-patch scale within mature stands. Finally, mature stands provide cone crops necessary to support red squirrels, which is an important alternate prey item in Colorado. We note that other life-history requirements (e.g., denning habitat, summer prey) may not be captured by these management recommendations for winter hunting habitat.

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